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Benthic–pelagic links: responses of benthos to water-column nutrient enrichment

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Abstract. Although the responses of pelagic algae and invertebrates to gradients of nutrient enrichment are well known, less is known about the responses of benthos to such gradients or how benthic and pelagic responses may interact. We performed a 9-wk experiment in 2000-L mesocosms in the field to test for the effect of water-column nutrient enrichment on phytoplankton, algae on sediments (epipelon) and hard surfaces (plastic strips), as well as pelagic and benthic primary consumers. The experimental design consisted of 4 nutrient enrichment rates (0, 0.5, 1.0 and 2.0 $\mu\text{g P L}^{-1} \text{ d}^{-1}$, together with N to yield an N:P ratio of 20:1 by weight). Nutrient enrichment induced significant increases in chlorophyll *a* in phytoplankton and attached algae, but not epipelon. Zooplankton biomass was significantly higher in enriched mesocosms than in controls over the initial 4 wk of enrichment, but the effect was not sustained over the course of the experiment. Densities of sediment-dwelling, and hard-substrata-associated invertebrates were higher in enriched treatments relative to controls. Emergence of benthic insects also increased with enrichment. Size and species composition of benthic macroinvertebrates differed between enriched treatments and controls. Our results suggest that nutrients added to the water column were quickly converted into benthic biomass, likely reducing pelagic responses to enrichment.

Key words: nutrient enrichment, mesocosm, benthic–pelagic links, periphyton, macroinvertebrates, Chironomidae.

The outcome of competition for resources is often linked to the spatial position of the competitors relative to resource distribution (Campbell et al. 1991). In lentic systems, benthic and planktonic habitats are physically juxtaposed, generating the potential for several modes of interaction via resource use. Despite the fact that manipulations of resources in lake habitats often have rapid direct effects in both habitats, and easily recognized indirect links between the two (Threlkeld 1994), benthic and pelagic communities are typically studied as if their spatial segregation makes them functionally independent (Boero et al. 1996, Lodge et al. 1997). The potentially compensatory interactions between benthic and pelagic communities in response to nutrient loading have not been extensively studied (Lodge et al. 1988, Scheffer et al. 1993).

Algae potentially compete for light and nutrients, which are differentially distributed within lakes (Sand-Jensen and Borum 1991). At-

tached and planktonic algae in lakes share a common light source, but they do not necessarily use the same nutrient pools. In productive lakes, phytoplankton may reduce light penetration, limiting autotrophic growth of attached algae. Competition for nutrients among algae in non-light-limited lake habitats is less clear due to different potential nutrient sources. Like phytoplankton, periphyton on firm, chemically inert substrata (e.g., epilithon) sequester nutrients from the water column, creating potential for competition with phytoplankton. In contrast, periphyton on sediments (epipelon) may derive nutrients from this substratum, and potentially regulate the availability of these nutrients to phytoplankton (Carlton and Wetzel 1988, Hansson 1990, Sundbäck et al. 1991, Rizzo et al. 1992).

Benthic and pelagic consumers respond to and may modify autotrophic responses to nutrient enrichment (Leibold and Wilbur 1992). Zooplankton may benefit from and regulate nutrient-induced stimulation of phytoplankton production (Vanni 1987, Carpenter et al. 1996). Similarly, benthic herbivores may benefit from

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and regulate increases in periphyton biomass (Cattaneo 1983, Mazumder et al. 1989a, Rosemond et al. 1993). Many benthic consumers may also benefit from increases in phytoplankton biomass or production (Davies 1980, Welch et al. 1988) by filter feeding or collecting newly sedimented phytoplankton (Jonasson 1972, Johnson et al. 1989, Lindegaard 1994). The availability of phytoplankton to benthic consumers is modified by zooplankton grazing; reduced zooplankton biomass may result in increased sedimentation of high quality food to benthic consumers (Kajak 1988, Mazumder et al. 1989b).

These many potentially strong links between benthic and pelagic communities suggest that it may be misleading to focus only on responses of benthic or pelagic communities to resource perturbations (Threlkeld 1994) without assessing inter-habitat interactions. Nutrients added during enrichment may accumulate in the benthos via direct uptake by periphyton (Phillips et al. 1978, Brönmark and Weisner 1992, Scheffer et al. 1993, Axler and Reuter 1996, Havens et al. 1996) or by invertebrates feeding on suspended or sedimented algae (Dermott et al. 1977, Kajak 1988, Kornijów and Gulati 1992). The flow of nutrients to benthos may therefore reduce the nutrient subsidy to phytoplankton. Here we present results of a mesocosm experiment performed to determine responses of benthic and pelagic algae and invertebrates to a gradient of nutrient enrichment. We focus on benthic responses in asking whether producers and consumers in these two habitats respond similarly to enrichment.

Methods

Study site

Our experimental site was the shallow (mean depth = 2.3 m) central basin of Long Lake, an oligo-mesotrophic system at the University of Notre Dame Environmental Research Center (Gogebic County, Michigan: 46°14'N 89°30'W). Two types of substrata for periphyton growth predominate in this lake: soft, organic-rich sediments and fallen trees (woody debris). Aquatic macrophytes (primarily *Isoetes*, *Utricularia*, and *Sparganium*) are also present but not abundant (D. M. Lodge, unpublished data). During May–August of 1992 average conditions in the central basin of Long Lake were Secchi depth = 2.6 m,

water column chlorophyll *a* = 6 µg/L, total phosphorus (TP) = 11 µg/L, and an epilimnetic temperature range of 15–22°C (S. R. Carpenter, University of Wisconsin, unpublished data; *n* = 15 for each parameter). Background phosphorus loading into Long Lake was about 0.1–0.2 µg P L⁻¹ d⁻¹ (Carpenter et al. 1996).

Experimental design

Our design employed mesocosms suspended from rafts (4 mesocosms/raft) floating in 2 m of water. Individual mesocosms were subjected to one of 4 nutrient treatments (3 replicates of each), with treatments randomly assigned to locations on the rafts. Mesocosms were composed of translucent plastic formed as open-ended cylinders with a 1-m² cross-sectional area and a volume of 2000 L. An iron hoop at the bottom of each mesocosm was embedded 0.3 m into the sediments. Plastic hoops at the middle and top of the cylinder maintained mesocosm shape. Mesocosms were filled with lake water filtered through 100-µm mesh to remove crustacean zooplankton. To homogenize zooplankton assemblages among mesocosms, zooplankton were collected from Long Lake with vertical tows of an 80-µm conical net and pooled into a single container. After removing *Chaoborus* larvae from the container with a pipette, we added ≈44 µg dry weight/L equivalents of zooplankton to each mesocosm, which was 50% of the mean mid-summer zooplankton biomass in Long Lake during the previous year (1991). The assemblage added to the mesocosms was dominated by large cladocerans (*Daphnia rosea*, *D. pulex*, and *Holopedium gibberum*) and cyclopoid copepods (*Orthocyclops modestus* and *Cyclops vernalis rubellus*) (Cottingham et al. 1997).

Each day from 12 June through 7 August 1992, we added a concentrated solution of Na₂HPO₄ and NH₄NO₃ to 3 sets of mesocosms to obtain daily loading rates of 0.5 µg P/L with 10 µg N/L, 1 µg P/L with 20 µg N/L, or 2 µg P/L with 40 µg N/L. This N:P ratio approximated the ratio in the lake. A 4th set of mesocosms served as an unenriched control. Hereafter, we identify these treatments by their addition rate of P (0.0, 0.5, 1.0, and 2.0 µg P L⁻¹ d⁻¹). We focus on phosphorus rather than nitrogen because it is this nutrient that limits phytoplankton growth in our study system and oth-

er lakes in the same geographic region (Carpenter and Kitchell 1993). Immediately following daily nutrient additions, we gently mixed the water column in all mesocosms (including controls) by lowering a Secchi disk to 1.25 m and slowly pulling it back towards the surface. Visual inspection showed that this method did not disturb the sediments.

Because the morphometry of our mesocosms overrepresented surfaces for attached algae (including mesocosm walls) relative to deep lakes, we scrubbed the inner sides of the mesocosms on 6 July (week 4) to reduce buildup of periphyton. This procedure probably resulted in a short-term pulse of nutrients but did not produce any sustained increase in water-column chlorophyll.

Pelagic responses: nutrients, autotrophs, and invertebrates

Depth-integrated samples from the water column of each mesocosm for soluble reactive phosphorus (SRP), total phosphorus (TP), phytoplankton chlorophyll *a*, and zooplankton were taken weekly and before daily nutrient additions using a 1.5-m-long PVC pipe (5 cm diameter) with a rubber stopper. Samples for SRP were filtered through Whatman GF/F filters into a flask and frozen for 3 d before analysis. TP samples were frozen and later digested with ammonium persulfate before analysis. All concentrations were then determined with an autoanalyzer. Phytoplankton chlorophyll *a* samples were filtered onto a Whatman GF/F filter, frozen for at least 24 h, then extracted with methanol and analyzed by fluorometry (Marker et al. 1980). Weekly zooplankton samples were obtained using the same PVC pipe sampling device and filtering water from 3 pooled, depth-integrated samples through an 80- μ m mesh in the field. Zooplankton in each sample were then filtered onto a dried and tared Whatman GF/F filter, dried, and reweighed to determine total zooplankton biomass.

Benthic autotrophs

We measured periphyton as chlorophyll *a* on the sediments (epipelic) and on 5 cm \times 2 m strips of plastic mesocosm material (epiplastic) used as an analog for hard substrata such as woody debris. On 13 June, 3 plastic strips were

weighted at one end and hung from the middle of a removable PVC rod centered across the top of each mesocosm. The broad surfaces of the plastic strips faced north and south. All strips were temporarily removed and placed in the lake adjacent to the enclosures when the mesocosm walls were scrubbed. Disturbance of the attached communities during the transfer was minimal. One strip from each mesocosm was removed for sampling on 13 July, 26 July, and 8 August (weeks 5, 7, 9). After removal, 2–5-cm segments were cut from each strip at depths of 0.05 m, 0.50 m, and 1.50 m. Each strip segment was extracted in methanol and analyzed for chlorophyll *a* as described for phytoplankton. Chlorophyll *a* concentration (mg/m²) was calculated by dividing by the surface area of both sides of the extracted strip segment (i.e., length \times width \times 2). To calculate total chlorophyll on the mesocosm walls at the end of the experiment, we first estimated a single average depth-integrated chlorophyll *a* concentration (mg/m²) for each mesocosm. This was calculated by plotting measured chlorophyll *a* concentrations on strips against depth and integrating the area beneath the curve. The depth-integrated value was then multiplied by 7.1 m² (the surface area of mesocosm walls) to obtain total epiplastic chlorophyll. Because we scrubbed walls and not strips, total wall chlorophyll at the end of the experiment may be overestimated.

We sampled epipelagic algae from plastic beakers (7.6 cm diameter, 500 mL) modified to hold sediments while allowing interchange of interstitial water. Three 30-cm² windows were cut in the sides of each beaker and covered with 150- μ m Nitex mesh. Three 2.5-m pieces of lightweight nylon rope were attached at equal distances around the rim of each beaker and tied together at their opposite ends. On 15 June sediment cores were collected, using SCUBA, near the mesocosms using a PVC corer with the same diameter as the beakers, and the intact sediment cores were transferred to individual beakers. From the water surface, we lowered 2 beakers into each mesocosm using the attached ropes and a flat disk attached to a PVC pole. We stabilized the beakers during lowering by maintaining a slight upward pressure on the ropes and simultaneously pushing downward on the disk which was placed over the mouth of the beaker. When the beaker reached the bottom, we gently pushed it into the sediments with the

disk, while maintaining upward pressure on the ropes. The ropes were hooked on to the side of the raft to facilitate beaker retrieval. To prevent contamination of epipelagic samples by epipelagic periphyton, all beakers were removed from the mesocosms and placed in the lake for 24 h when the mesocosm walls were scrubbed. Neither the removal nor the brief period in the lake had any visible effect on the epipelagic mat, which was well developed and appeared stable. Near the conclusion of the experiment, on 31 July (wk 8), beakers were retrieved from mesocosm bottoms and we took a 2-cm deep sediment core from each using a cut-off 60-cc syringe (inner diameter 2.6 cm). The entire core was placed in an opaque film canister, frozen and lyophilized (Hansson 1988) before analysis for chlorophyll *a* content as described above.

Benthic invertebrates

Abundance and taxonomic composition of benthic invertebrates in the sediments and on the mesocosm strips were sampled near the end of the experiment. Sediment-dwelling macroinvertebrates were sampled from each mesocosm on 31 July (wk 8) by collecting duplicate sediment cores (core area = 45.6 cm²; coring depth = 10–20 cm) immediately following removal of epipelagic beakers. With few exceptions, this coring depth is adequate to sample benthic macroinvertebrates (Heinis et al. 1994, Takacs and Tokeshi 1994). For macroinvertebrates on strips, we sampled additional segments of the same plastic strips used for sampling epipelagic algae. On 26 July (wk 7), one strip from each mesocosm was cut into a lower near-sediment portion (from 1.50 m water depth to the lake bottom) and an upper near-surface portion (0.05–0.50 m water depth). The attached material was removed with a nylon brush and sieved through 243- μ m mesh, and the animals collected were preserved in 70% ethanol. Head-capsule width for Diptera and body length for all other taxa were measured at 24 \times with an ocular micrometer. These measurements were converted to dry weight using regressions in Meyer (1989) for oligochaetes and in Smock (1980) for all other taxa.

Insect exuviae floating in the mesocosms were collected with a 243- μ m mesh net on 26 June, 10 July and 27 July (weeks 3, 5, 7) to assess differences in insect emergence among treat-

ments. Because it is unlikely that all insect exuviae remained floating between our sampling dates (Coffman 1973), the numbers of exuviae collected are used only for comparisons among treatments. Genera of Chironomidae emerging from the mesocosms were qualitatively determined by inspection of collected exuviae using keys in Wiederholm (1986).

Statistics

Analyses of variance were performed using Systat (SYSTAT Network version 5.02 for DOS, SYSTAT Inc., Evanston, Illinois). Nutrient concentrations, phytoplankton chlorophyll *a*, and total zooplankton biomass were analyzed by repeated measures analysis of variance (RM ANOVA) for the main effect of nutrient-loading rate (Winer 1971, Gurevitch and Chester 1986). Epipelagic chlorophyll *a* was analyzed by a 2-way RM ANOVA for the main effect and interactions of depth and nutrient-loading rate. Differences among treatments in epipelagic algal chlorophyll *a*, sediment and epipelagic invertebrate density and biomass, and total number of insect exuviae were analyzed with 1-way ANOVA. Residuals of all ANOVAs were checked for normality using normal probability plots. Response variables were log transformed to normalize residuals and equalize variance among treatments when necessary. For 3 benthic invertebrate responses (density of sediment-dwelling invertebrates, exuviae number, and proportion of Chironomina in sediment samples), ANOVA results suggested no significant effect of enrichment. However, because we were primarily interested in controls versus enriched treatments, which were similar but had high within-group variation, we conducted a linear contrast (LC) that compared the control mean to the pooled mean of the 3 enriched treatment levels (Sokal and Rohlf 1981 pp 530–539, Wilkinson 1989).

Results

Pelagic responses: nutrients, autotrophs, and invertebrates

Nutrient enrichment produced significantly higher water column TP (17.84 ± 7.04 , 20.77 ± 5.24 , 21.32 ± 6.02 , 25.37 ± 3.01 ; mean $\mu\text{g/L} \pm 1 \text{ SD}$, in 0.0, 0.5, 1.0, and 2.0 $\mu\text{g PL}^{-1} \text{ d}^{-1}$ treatments respectively; ANOVA $p = 0.002$, Fig. 1a),

and phytoplankton chlorophyll *a* (5.41 ± 2.70 , 6.11 ± 2.20 , 9.73 ± 1.96 , 9.50 ± 1.65 ; mean $\mu\text{g/L} \pm 1$ SD, RM ANOVA $p = 0.047$, Fig. 1b). SRP did not increase significantly with nutrient enrichment (RM ANOVA $p = 0.400$). Although total zooplankton biomass quickly increased after initial seeding and was higher with enrichment over the 1st 4 wk of the experiment (301 ± 55 , 484 ± 68 , 673 ± 224 , 607 ± 78 ; mean $\mu\text{g dry mass/L} \pm 1$ SD, RM ANOVA $p = 0.014$), no significant difference between enriched treatments and the control was detected when all sampling dates were included in the analysis (344 ± 99 , 524 ± 114 , 588 ± 237 , 531 ± 37 ; mean $\mu\text{g/L} \pm 1$ SD, RM ANOVA $p = 0.122$). Additional information on pelagic responses is provided in Cottingham et al. (1997).

Benthic autotrophs

Epiplastic chlorophyll *a* was higher in all enriched mesocosms relative to controls, with the degree of increase positively related to nutrient addition rate (RM ANOVA $p < 0.001$, Fig. 1c), and depth (RM ANOVA $p = 0.003$). No significant interactions were detected between these effects (RM ANOVA nutrient \times depth $p = 0.380$), nor nutrient addition rate and time (RM ANOVA $p = 0.314$). Epipellic chlorophyll *a* did not respond to nutrient addition (ANOVA $p = 0.698$; Fig. 2). As an index of the relative accumulation of nutrients in phytoplankton, in epiplastic algae (as determined from areal abundance on strips), and in epipellic algae at the end of the experiment, we calculated total chlorophyll in each of these compartments on a whole mesocosm scale (Fig. 2). Epipellic algae were the largest store of chlorophyll *a* in control mesocosms (50.2%), whereas most of the increase in total mesocosm chlorophyll with enrichment was epiplastic (58.4% at the highest nutrient loading rate). The highest mean epipellic chlorophyll *a* density among all treatments at the end of the experiment was in controls (24.7 mg/m^2). However, averages of chlorophyll *a* densities among enriched mesocosms were much higher relative to controls in phytoplankton (15.7 vs. 7.7 mg/m^2) and epiplastic algae (7.1 vs. 2.4 mg/m^2).

Benthic invertebrates

The density of sediment-dwelling invertebrates was significantly higher in enriched me-

socosms than in controls (ANOVA $p = 0.211$; LC comparing control with the pooled mean of nutrient enriched treatments, $p = 0.045$; Fig. 3a). Although mean biomass of sediment-associated invertebrates was $5.6\times$ higher in fertilized treatments than in controls, this difference was not statistically significant because of high variation among replicates in enriched treatments (ANOVA $p = 0.315$, LC $p = 0.079$). Densities of macroinvertebrates on strips increased with nutrient enrichment rate (ANOVA $p = 0.008$) and depth (ANOVA $p = 0.025$, Fig. 3b). Numbers of collected insect exuviae doubled in response to fertilization (ANOVA $p = 0.207$, LC $p = 0.052$, Fig. 3c). Chironomid taxa represented as collected exuviae included genera from the subfamilies Tanypodinae (*Ablabesmyia*, *Clinotanypus*, *Labrundinia*, *Nilotanypus*, and *Procladius*), Orthocladiinae (*Corynoneura*, *Nanocladius*, and *Psectrocladius*), and Chironominae (Tribe Chironomini: *Chironomus*, *Cladopelma*, *Dicrotendipes*, *Endochironomus*, *Microtendipes*, and *Polypedilum*; Tribe Tanytarsini: *Tanytarsus*).

Taxonomic composition of benthic invertebrates sampled from mesocosms differed among substrata, and appeared sensitive to enrichment. At the end of the experiment, Chironomini (Diptera: Chironomidae) constituted 43% of sediment-dwelling invertebrates in fertilized treatments (45%, 45%, and 40% in the 0.5, 1.0, and $2.0 \mu\text{g P L}^{-1} \text{ d}^{-1}$ treatments, respectively), but only 7% in the unenriched control (ANOVA $p = 0.179$, LC $p = 0.037$; Fig. 4c). This contrast is also reflected in the size-frequency distributions of sediment-dwelling Chironomidae, which also differed among treatments (Fig. 5). Sediments in enriched mesocosms supported greater proportions of large Chironomini (mean head capsule width = 0.407 mm) relative to the smaller Tanytarsini (mean head capsule width = 0.177 mm), as evident from the bimodal distribution of chironomid head capsule widths in fertilized treatments relative to controls where the larger Chironomini are much less abundant (Figs. 4c, 5).

Distribution of invertebrates on plastic strips was segregated vertically, with less evidence of a nutrient effect on taxonomic structure than observed in sediment-associated assemblages. Invertebrate assemblages on near-sediment strip portions were similar to those within the sediments of fertilized mesocosms, while near-surface portions of strips supported a high pro-

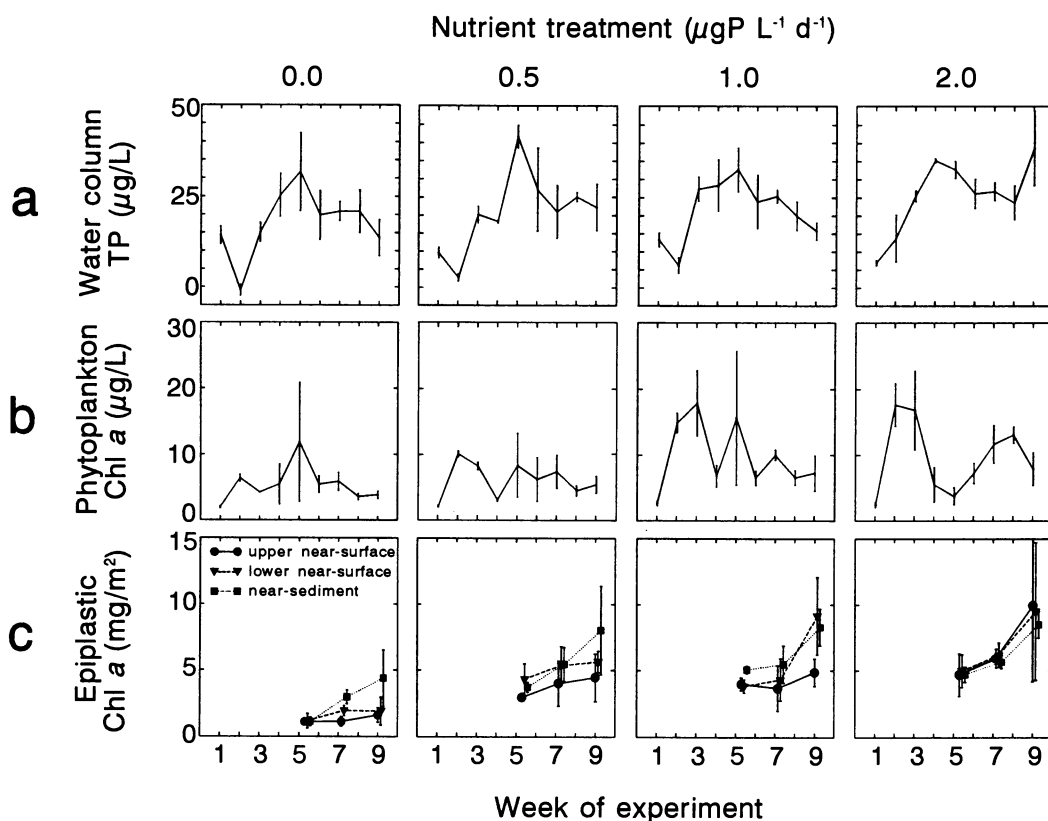


FIG. 1. Mean (± 1 SD) responses over time to different nutrient treatments (columns) of (a) water column total phosphorus (TP), (b) phytoplankton chlorophyll *a*, and (c) chlorophyll *a* in epiphytic algae, estimated from plastic strips of mesocosm material hanging in mesocosms. Line and symbol combinations refer to samples taken from different depths: upper near-surface = 0.05 m, lower near-surface = 0.50 m, near-sediment = 1.50 m.

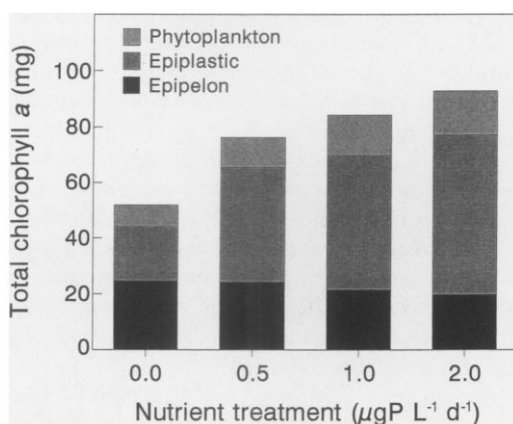


FIG. 2. Total chlorophyll *a*/mesocosm by algal group at the end of the experiment. Epiphytic chlorophyll represents algae growing on mesocosm walls as estimated from depth-integrated densities on plastic strips hanging in mesocosms.

portion of orthoclads, primarily *Psectrocladius* and *Corynoneura*, (near-surface: 56.5%; near-sediment 21.5%; dependent *t*-test = 3.991; $p = 0.002$; Fig. 4) which were rare in sediment samples.

Invertebrate biomass on strips was positively correlated with epiphytic chlorophyll *a* in near-surface samples ($r = 0.837$, $p = 0.001$), but not in near-sediment samples ($r = 0.173$, $p = 0.584$; Fig. 6). The ratios of macroinvertebrate biomass to chlorophyll *a* on strips did not differ with nutrient addition rates on either near-surface ($r = 0.249$, $p = 0.697$), or near-sediment ($r = 0.104$, $p = 0.747$) strip portions.

Discussion

Most previous experiments incorporating both benthic and pelagic responses to enrich-

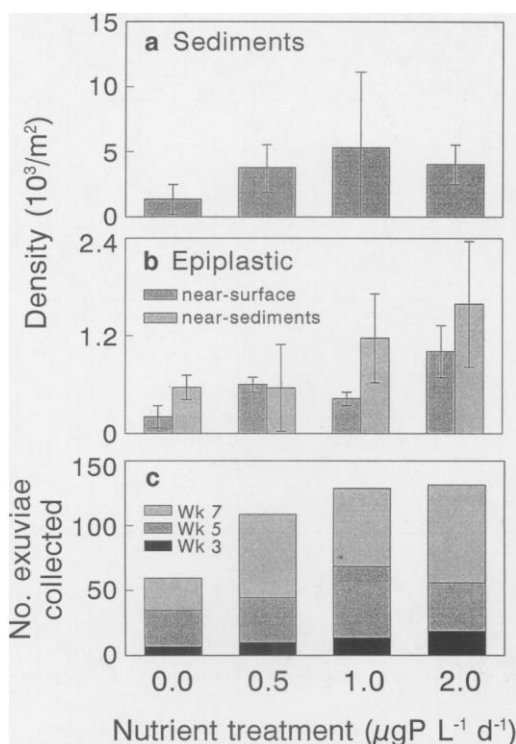


FIG. 3. Benthic macroinvertebrate responses to nutrient addition, assessed at the end of the experiment. (a) Mean density (± 1 SD) of sediment-dwelling macroinvertebrates. (b) Mean density (± 1 SD) of near-surface (0.05–0.50 m depth) and near-sediment (1.50 m depth–sediments) epiplastic macroinvertebrates. (c) Total number of insect pupal exuviae collected from water surface on 3 sampling dates for each nutrient treatment.

ment have focused on fewer responses or have not included a gradient of nutrient addition rates (e.g., Mazumder et al. 1989a, Hershey 1992, O'Brien et al. 1992). Thus, our experiment provided a unique opportunity to test responses of the benthic community to a range of nutrient loading rates, and to compare the relative magnitude of benthic and pelagic responses.

Potential interaction of pelagic and benthic autotrophs

Responses by benthic autotrophs to enrichment varied with substratum type. Epiphytic algae responded positively to increased phosphorus supply rates, suggesting a high rate of accumulation of phosphorus that might otherwise

be available to phytoplankton. High zooplankton biomass and dominance by large *Daphnia* may limit the magnitude of increase in phytoplankton chlorophyll *a*, but increases in zooplankton biomass following initial seeding were modest and short-lived, suggesting that phosphorus was not greatly accumulating in pelagic organisms. The accumulation of chlorophyll in epiphytic algae greatly exceeded that in epiphyton and phytoplankton, suggesting a strong potential for nutrients to accumulate in periphyton on hard surfaces with abundant light, lessening phytoplankton response. Our ability to detect differences in epiphytic chlorophyll *a* among treatments was probably augmented by providing a bare, uncolonized substratum, in contrast to epiphyton which was abundant at the outset of the experiment. However, epiphytic chlorophyll *a* densities in near-surface portions of strips in enriched treatments increased throughout the experimental period, which was not the case in control treatments. The patterns of epiphytic chlorophyll *a* accumulation among treatments over time suggests that the contrasts among treatments and storage of P as epiphytic chlorophyll may have been greater over a longer experimental period.

In contrast, where periphyton are light-limited, shading induced by high phytoplankton density may negatively affect benthic chlorophyll (Mazumder et al. 1989a, Marks and Lowe 1993, Havens et al. 1996). However, chlorophyll is an imperfect index of algal biomass when comparisons are made among communities experiencing different ambient light environments (Kirk 1994) because algae will increase chlorophyll-to-biomass ratios in low light environments. Due to the potential for phytoplankton to reduce light availabilities in the enriched mesocosms, our chlorophyll-based periphyton results must be assessed with caution. Nevertheless, the visual appearance of the strips and the moderate increase in phytoplankton relative to many enrichment studies suggest that our chlorophyll results are indicative of an actual increase in epiphytic biomass.

Visually, the thickness and structure of the epiphytic algal mat changed with depth. Toward the surface, filamentous forms dominated while a thicker more gelatinous mat was characteristic on near-sediment strip portions. Chlorophyll increased with depth in the control and all 3 enriched treatments, and there was no

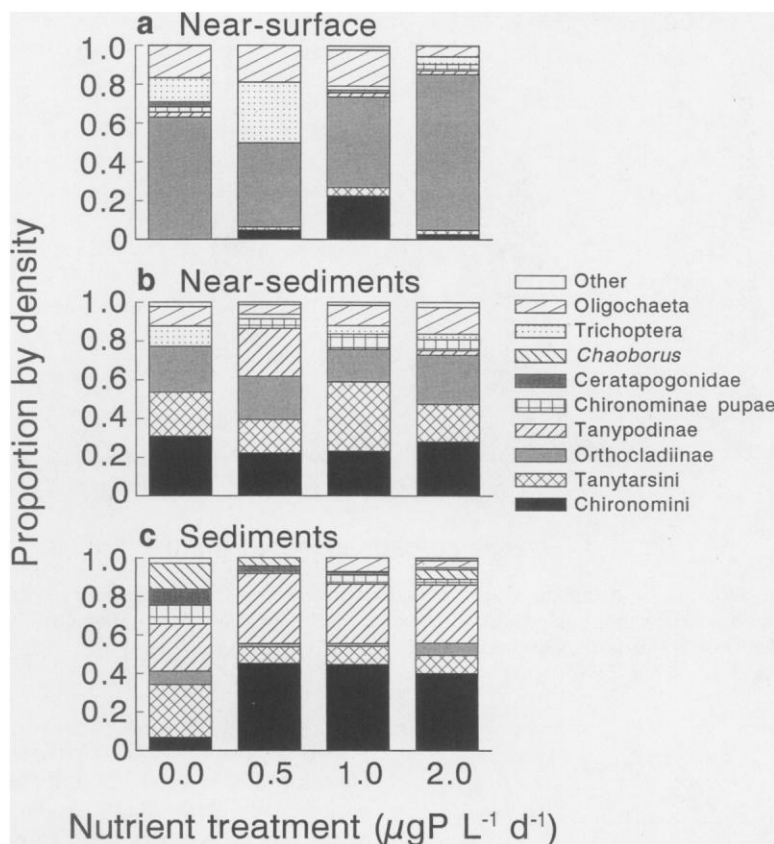


FIG. 4. Proportions (per density) of macroinvertebrate taxa in each nutrient treatment on (a) near-surface (0.50–0.50 m) portions of strips, (b) near-sediment (1.50 m-sediments) portions of strips, and (c) in sediments. Diptera include pupae of Chironomidae, larvae of Ceratopogonidae, *Chaoborus*, subfamilies of Chironomidae (Orthoclaadiinae, Tanypodinae, and Chironominae), and tribes of Chironominae (Chironomini and Tanytarsini). Annelids were represented by the class Oligochaeta. "Other" includes *Sialis* (Megaloptera), Odonata, and Bivalva.

depth \times nutrient interaction. Also, the phytoplankton response and maximum P loading rate were moderate relative to other enrichment studies (Hall et al. 1970, Nilsson et al. 1991, Fong et al. 1993, Havens et al. 1996), and the reduction in light was not likely to overcome nutrient limitation in a 2-m-deep environment.

We did not detect a response of epipelagic algae to nutrient addition. As noted for epiplastic algae, an increase in chlorophyll *a* in the sediments could have indicated either a positive (through an increase in biomass) or negative (through an increase in biomass-specific chlorophyll due to acclimation to lower light) response of algae. The lack of response was in marked contrast to the positive response by

phytoplankton and epiplastic periphyton chlorophyll *a*. It is possible that epipelon on the mat surface (which account for most of the production within the mat) responded to enrichment, but any increase at the surface was masked by extracting a 2-cm core and thus including non-photosynthesizing chlorophyll *a* deeper in the sediments. However, whole-lake fertilizations of central Long and nearby lakes have corroborated the lack of response by epipelagic algal chlorophyll *a* (in the top 5 mm) and primary production (Vadeboncoeur and Lodge, unpublished data). The different responses of epipelagic and epiplastic periphyton are consistent with recent studies that suggest that epipelagic algae on highly organic sediments sequester nutrients from

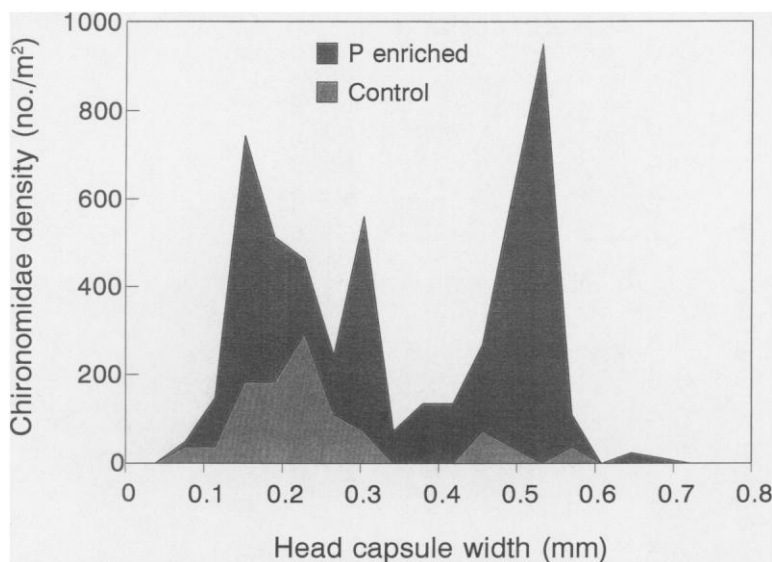


FIG. 5. Distribution of head capsule widths of sediment-dwelling Chironomidae in control and enriched treatments (enriched treatments pooled). Head capsule widths are used as an allometric indicator of total body size. Differences in this parameter between control and enriched treatments are partly due to contrasts in taxa (Fig. 4a).

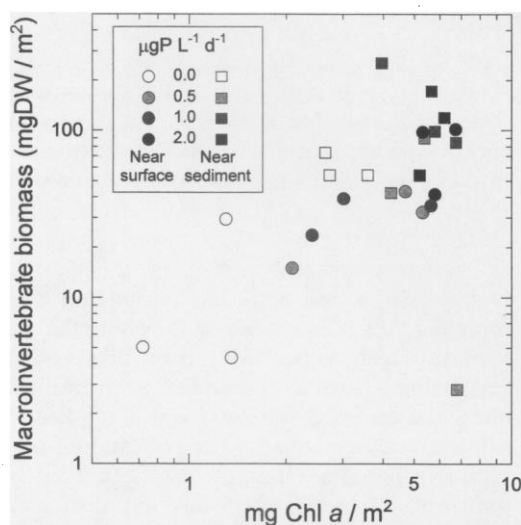


FIG. 6. Relationship of epiplastic macroinvertebrate biomass and chlorophyll *a* of epiplastic algae. Points represent means from nutrient treatments and near-surface (0.05–0.50 m, circles) or near-sediment (1.50 m-sediments, squares) areas. Correlation of macroinvertebrate and periphyton chlorophyll *a* is significant near-surface ($r = 0.837$, $p = 0.001$), but not near-sediment ($r = 0.173$, $p = 0.584$).

sediment pore water (Björk-Ramberg 1984, Hansson 1990), while periphyton growing on rocks, macrophytes, and sandy sediments are dependent on water column nutrients (Cattaneo 1987, Nilsson et al. 1991, Sand-Jensen and Borum 1991, Pinckney et al. 1995).

The relative contribution of phytoplankton to whole mesocosm chlorophyll varied little (13.2–15.6%) among loading rates. Overall, the distribution of chlorophyll between epipelton and epiplastic algae (and total chlorophyll) shifted markedly towards epiplastic algae with increased nutrient loading. The enrichment-induced increases in chlorophyll densities in epiplastic algae, but not epipellic algae, suggests that periphyton on hard, nutrient-inert surfaces are more sensitive to changes in water-column enrichment on an areal basis than periphyton on organic sediments. In lakes, the relative contribution of benthic chlorophyll to total chlorophyll within the system is negatively related to mean depth (Lodge et al. 1997). Although our mesocosms had high surface:volume ratios relative to deep lakes, most lakes in the world are shallow (Moss 1988) and have mean depths similar to or less than the depths in our experimental mesocosms, with abundant surfaces like mud, cobble, coarse woody debris, and macrophytes. Our re-

sults suggest that nutrient loading (at least within the range of our loading rates) in shallow lakes might shift abundance of total algae in favor of benthic algae on macrophytes or other hard surfaces (Sand-Jensen and Søndergaard 1981).

Responses of benthic consumers

Enrichment-induced increases in density of sediment-dwelling macroinvertebrates may have resulted from increased survival and growth of chironomids that were food-limited in unenriched mesocosms. Many chironomid species filter-feed directly on phytoplankton from the water column (Jonasson 1972, Johnson et al. 1989, Berg 1995), and/or collect newly sedimented algae (Lindegaard 1994, Yoshioka et al. 1994). Phytoplankton were present in the alimentary tracts of sediment-dwelling chironomids in enriched treatments. Subsequent whole-lake nutrient enrichments (including Long Lake; Carpenter et al. 1996) at rates within the range used in this experiment produced patterns of carbon and nitrogen stable isotope ratios which suggest that pelagic food resources become more important in the diets of macrobenthos with enrichment (Blumenshine, unpublished data). Another possibility is that epipelagic production enhanced by enrichment was grazed by the higher densities of chironomids in enriched treatments. However, we have additional evidence which suggests this was not a primary mechanism. When grazers were excluded, one of us found that epipelagic chlorophyll did not increase with nutrient additions (Vadeboncoeur, unpublished data), consistent with our interpretation that epipelagic did not respond to nutrient enrichment of mesocosms and that phytoplankton fueled the observed increases in sediment-dwelling invertebrates.

Size-distribution and taxonomic structure of chironomid assemblages in sediment samples were also affected by enrichment. Distribution of head-capsule widths of chironomids were bimodal in enriched treatments near the end of the experiment, with the mode consisting of larger individuals rare in control samples. The presence of an additional size class in enriched treatments apparently reflected increased survival or growth of Chironomini, and in large part accounted for the community shift and increased density in enriched treatments. We sus-

pect that differences among treatments were due to contrasts in survival or growth rates rather than increases in egg production within mesocosms, for example, because macroinvertebrate assemblages were dominated by insects with aerial adult stages.

The observed increase in rate of emergence of benthic insects with enrichment was consistent with previously documented positive relationships between emergence and phytoplankton productivity (Davies 1980, Welch et al. 1988). The rapid translation of increased autotrophic biomass into increased survival and emergence by sediment-dwelling chironomids has been previously documented for lakes (Welch et al. 1988) and streams (Mundie et al. 1991). Food level positively affected percent emergence, body size at emergence, and growth rate in laboratory-reared *Chironomus tentans* (Ball and Baker 1995). These earlier studies and our results suggest that in many, but not all (Hershey 1992) aquatic habitats, at least some taxa of benthic chironomids are food limited. In addition, the insect responses to enrichment we observed were likely underestimates because the methods used to measure benthic insect standing stock and emergence cannot wholly detect increases in production (Goedkoop and Johnson 1996).

Densities of macroinvertebrates on strips responded to nutrient-enhanced chlorophyll *a* more strongly than sediment-dwelling macroinvertebrates. Enrichment did not result in assemblage contrasts in controls and enriched treatments. Availability of a substratum other than sediments apparently increased the abundance of the orthoclad chironomids *Psectrocladius* and *Corynoneura* in all treatments. These genera are typically found on macrophytes (Kesler 1981, Fairchild et al. 1989, Botts and Cowell 1992), and were the most abundant taxa on near-surface portions of strips, but were rare in mesocosm sediments.

Interaction of benthic autotrophs and consumers

Community responses on strips differed by depth. Periphyton chlorophyll abundance was higher on near-sediment portions of strips, and macroinvertebrate assemblages at this depth were more similar to assemblages on sediments than those on near-surface portions of strips. Ratios of periphyton and macroinvertebrate biomass also varied with depth, but not with nu-

trient treatment. We detected a significant positive correlation between macroinvertebrate biomass and epiplastic chlorophyll *a* on near-surface portions of plastic strips, but not on near-sediment portions. These relationships suggest an aggregative response of grazers to attached algae, as found previously for invertebrates on macrophytes (Cattaneo 1983) and/or increased survival of the typically epiphytic midges as a function of widespread algal food. Macroinvertebrates likely responded, in part, to increases in epiplastic algae as habitat (review in Berg 1995). However, time lags and a relatively short experimental duration may have precluded detection of any negative effect of macroinvertebrate grazing on epiplastic algae (Cattaneo 1983, Mazumder et al. 1989a, Hann 1991).

We saw little or no difference in benthic invertebrate responses among enrichment levels of 0.5, 1.0 and 2.0 $\mu\text{g P L}^{-1} \text{d}^{-1}$. Our lowest enrichment level was 2.5 to 5-fold greater than background phosphorous loading rates (Carpenter et al. 1996). Benthic consumer assemblages adapted to oligo-mesotrophic conditions may have lags in responding to seasonal increases in nutrient loading rates above this level. Alternatively, benthic consumers may have been responding to the relatively small increases in total mesocosm chlorophyll among enriched treatments. The lack of graded responses may also result from the longer life cycles of benthic invertebrates relative to those in the plankton. Our measured responses were likely by one or two generations of benthic macroinvertebrates, whereas zooplankton could produce multiple generations over the experimental period.

Relevance of mesocosm results to natural lakes

Benthic responses could be reduced at the whole-lake scale by shading and by fish predation on macroinvertebrates. In nutrient-rich and/or deep lakes, retention of phosphorus in phytoplankton and subsequent shading of periphyton and macrophytes by phytoplankton may suppress benthic responses to enrichment in lakes with low grazing by zooplankton (Scheffer et al. 1993). Under other conditions, benthic algae may mediate fluxes of nutrients from sediments to the water-column. Benthic-feeding fish may limit increases in benthic invertebrate abundance as nutrient loading in-

creases (Mazumder et al. 1989a, Richardson et al. 1990, Hershey 1992). On the other hand, the generally long generation time of benthic relative to planktonic biota suggests that the results we induced by pelagic enrichment may be conservative with respect to longer term changes in shallow lake benthos. Overall, our results suggest that enrichment of shallow lakes may shift primary and secondary production away from phytoplankton and zooplankton toward benthos.

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